

Orthographic Priming in Braille Reading as Evidence for Task-specific Reorganization in the Ventral Visual Cortex of the Congenitally Blind

Katarzyna Rączy¹, Aleksandra Urbańczyk¹, Maksymilian Korczyk¹,
Jakub Michał Szewczyk¹, Ewa Sumera², and Marcin Szwed¹

Abstract

■ The task-specific principle asserts that, following deafness or blindness, the deprived cortex is reorganized in a manner where the task of a given area is preserved even though its input modality has been switched. Accordingly, tactile reading engages the ventral occipitotemporal cortex (vOT) in the blind in a similar way to regular reading in the sighted. Others, however, show that the vOT of the blind processes spoken sentence structure, which suggests that the task-specific principle might not apply to vOT. Strongest evidence for the

vOT's engagement in sighted reading comes from orthographic repetition-suppression studies. Here, congenitally blind adults were tested in an fMRI repetition-suppression paradigm. Results reveal a double dissociation, with tactile orthographic priming in the vOT and auditory priming in general language areas. Reconciling our finding with other evidence, we propose that the vOT in the blind serves multiple functions, one of which, orthographic processing, overlaps with its function in the sighted. ■

INTRODUCTION

A number of studies have put forth the idea that cortical regions might preserve their function even though their sensory modality has been switched. These studies used tasks that can be accomplished in more than one sensory modality, for example, both in the visual one and the tactile one. They provide ample evidence that the blind participants' ventral visual stream can perform tasks such as tactile and auditory object recognition (Amedi et al., 2007; Amedi, Malach, Hendler, Peled, & Zohary, 2001), auditory perception of body shapes (Striem-Amit & Amedi, 2014), tactile discrimination (Sadato et al., 1996), and tactile reading (Reich, Szwed, Cohen, & Amedi, 2011; Burton, Snyder, Conturo, et al., 2002). Auditory areas in the deaf, in turn, can be recruited for visual rhythm (Bola, Zimmermann, et al., 2017) and visual face recognition (Benetti et al., 2017). These studies suggest that, as a rule, the deprived cortical areas preserve their task specificity (Amedi, Hofstetter, Maidenbaum, & Heimler, 2017; Merabet & Pascual-Leone, 2010).

However, this rule sometimes seems to be violated, as the deprived areas can also take on new functions. The retinotopic and occipitotemporal visual cortices in the blind are activated during verb generation (Amedi, Raz, Pianka, Malach, & Zohary, 2003), and TMS of this brain

region disrupts verbal performance (Amedi, Floel, Knecht, Zohary, & Cohen, 2004). The visual cortex in the blind is activated for verbal memory tasks (Amedi et al., 2003), spoken sentence processing (Lane, Kanjlia, Omaki, & Bedny, 2015; Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011), and math processing (Kanjlia, Lane, Feigenson, & Bedny, 2016). In the deaf, in turn, the left auditory cortex shows increased activation to visuospatial working memory tasks with non-verbal stimuli (Ding et al., 2015). The question then is to what extent the deprived areas preserve their function and to what extent they acquire new ones.

Here, the study of orthographic processing in the blind could be illuminating. The visual word form area (VWFA) is an area in the left ventral occipitotemporal cortex (vOT) in sighted participants, which is activated in response to written orthographic stimuli (Dehaene & Cohen, 2011; Price & Devlin, 2011). Below, we refer to the vOT as an anatomical region and to the VWFA as a functional region that is characteristic of sighted participants.

When acquiring a written language, the brain becomes more efficient at processing recurring visual patterns of this language represented in its orthographic structure. In a process akin to statistical learning (Saffran, 2003), an English language readers' brain will learn that letters "th" occur frequently together, whereas letters "szw" never do so, and a Polish language readers' brain will learn the opposite. Letters embedded in frequently occurring

¹Jagiellonian University, Krakow, Poland, ²Institute for the Blind and Partially Sighted Children, Krakow, Poland

letter strings (“t” as in letter string “tion”) will begin to be processed more easily than letters embedded in infrequent letter strings (“t” in “txcf”; Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; McClelland & Rumelhart, 1981; Reicher, 1969). Previous studies have demonstrated that the VWFA in the sighted is tuned to the frequency of letter combinations occurring in the readers’ language (Vinckier et al., 2007; Binder et al., 2006; Dehaene, Cohen, Sigman, & Vinckier, 2005; Whitney, 2001). This tuning of the VWFA to the sublexical orthographic structure of written language is considered a hallmark of orthographic processing.

Preliminary reports have suggested that, when reading by touch (braille), congenitally blind participants show an activation of the vOT that is similar in its properties to the VWFA (Reich et al., 2011; Büchel, Price, Frackowiak, & Friston, 1998; Sadato et al., 1996). However, others have reported that the vOT takes on new higher cognitive functions, namely language processing (Lane et al., 2015; Bedny et al., 2011; Reich et al., 2011; Röder, Stock, Bien, Neville, & Rösler, 2002), and becomes activated when blind participants make semantic decisions about single words or listen to spoken sentences. Activation within the vOT is greater for lists of words than for lists of nonwords and larger for sentences than for lists of words (Lane et al., 2015; Bedny et al., 2011). The blind participants’ vOT also responds more to syntactically complex sentences (Kim, Kanjlia, Merabet, & Bedny, 2017). It remains thus unresolved whether the vOT in the blind preserves its reading function, that is, whether it is sensitive to the sublexical orthographic structure of braille stimuli or instead takes on a new role in abstract higher level cognitive functions (Bedny, 2017). The strongest evidence for the central role of the VWFA in reading in the sighted comes from intracranial recordings (e.g., Perrone-Bertolotti et al., 2014; Hamamé et al., 2013; Nobre, Allison, & McCarthy, 1994) and repetition suppression studies (Glezer, Kim, Rule, Jiang, & Riesenhuber, 2015; Glezer, Jiang, & Riesenhuber, 2009; Dehaene, Le Clec’h, Poline, Le Bihan, & Cohen, 2002). Repetition suppression (also known as priming) refers to a decreased neural response to a stimulus when the target stimulus (e.g., NURSE) is preceded by another prime stimulus similar semantically (e.g., DOCTOR) or orthographically (PURSE). Repetition suppression in the VWFA decreases with increasing dissimilarity between the two stimuli, indicating its tuning to the sublexical structure of letter strings. Thus, pairs of identical pseudowords have maximum overlap and evoke strongest suppression, pseudoword pairs with 1-letter difference (POAT–SOAT) have partial overlap and evoke less suppression, and two different pseudowords have no overlap and evoke no suppression (Glezer et al., 2009, 2015). We reasoned that if we can observe such a repetition suppression effect with braille, it would constitute evidence that the vOT of the blind plays an important role in tactile reading. Our prediction was that if the vOT in the blind subserves orthographic

processing, that is, if it is tuned to the sublexical orthographic structure of braille stimuli, it should exhibit repetition suppression for similar pseudowords presented in the tactile modality, but not in the auditory modality. This effect should be specific to the tactile domain only and should be distinguishable from repetition suppression to the same stimuli presented in the auditory modality, which according to previous reports can be observed in both sighted (Vaden, Muftuler, & Hickok, 2010; Cohen, Jobert, Le Bihan, & Dehaene, 2004; Dehaene et al., 2002) and blind (e.g., Arnaud, Sato, Ménard, & Gracco, 2013) participants in the STS, a multimodal area engaged in general language processing.

METHODS

Participants

Fifteen right-handed congenitally blind native Polish speakers (aged 18–42 years) participated in the experiment. Because this article, like almost all fMRI works published, relies on whole-brain analysis, two of these participants were excluded for reasons we outline below. In the congenitally blind, the left lateralization of frontotemporal language network is greatly reduced compared with sighted participants (Lane et al., 2017; Röder et al., 2002; Karavatos, Kaprinis, & Tzavaras, 1984), a phenomenon that also applies to right-handed persons. In individuals who have right-lateralized language networks in the frontotemporal cortices, reading and language responses in occipital areas are also right-lateralized (Lane et al., 2017; Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008). For consistency of whole-brain group analysis (see Figure 4), which cannot accommodate differences in laterality, we decided a priori to exclude participants with a strong right-hemisphere lateralization of language networks. To this aim, we applied a blind procedure in which laterality was judged by an independent coder not involved in the study. Participants were judged as having a right-lateralized language network if their peak Z score in the right vOT for the words versus rest contrast was at least 30% higher than in the corresponding left hemisphere region. The two participants were excluded according to this procedure. To ensure that the exclusion of these participants did not affect the overall outcome, we performed an additional ROI analysis in which data from right-hemisphere vOT ROIs from these two participants was included in the analysis. This confirmed that the overall results remained the same as without these two participants (see ROI Analysis section). Data from 13 participants (seven women, age range = 19–34 years) were included in the final analysis. Note that, given that blind participants are a hard-to-find clinical population, such a sample size is generally considered adequate in MRI studies of the blind (e.g., 10 participants in Kim et al., 2017, or 9 participants in Abboud, Maidenbaum, Dehaene, & Amedi, 2015).

The participant sample included three final-year high school students, one high school graduate, two university students, and seven postgraduates (2–5 years of studies). They were all blind from birth and had no visual experience, in particular no visual experience with letter shapes (for the detailed description, see Table 1). They were either completely blind ($n = 5$) or had primitive sensitivity to light. The main causes of blindness among the participants included retinopathy of prematurity ($n = 7$), toxoplasmosis ($n = 1$), and atrophy of the optic nerve ($n = 5$). Seven of the 13 participants read with their left hand despite being right-handed. A preference toward reading braille with the nondominant hand is a common and well-described phenomenon (Millar, 1997), although its cause is far from clear. Although some previous reports do not provide information about the reading hand, for those who do report it (Beisteiner et al., 2015; Burton, Sinclair, & Agato, 2012) the proportion of left-hand readers to right-hand readers is similar to that found in our group. The study was approved by the Jagiellonian University Ethics Committee. Written informed consent was obtained from all participants before the experiment. Participants were reimbursed for taking part in the study.

Braille Reading Speed Tests

Two different tests were used to test the participants' tactile reading speed before the study. Because no standardized tests measuring braille reading speed exist in Polish, we used the "Konopnicki test," a standard reading speed test used to estimate sighted children's reading speed that comprises 116 two- to six-letter-long single words. The test was printed in braille on sheets of A4 paper. The participants were asked to read aloud as many words

as possible in 60 sec. The experimenter counted how many words the participants were able to read accurately. Second, we used a test previously designed by Bola and colleagues (2016), which consists of a 400-word passage printed in braille from the book "Farsa Panny Heni" by Maria Rodziewiczówna. After having read the text silently, participants were given a test (printed in braille) consisting of 10 multiple-choice questions concerning the text. Participants then verbally gave answers to the experimenter. The overall time needed to read the text and the accuracy of the answers were measured.

Stimuli

Similar to other reading studies (e.g., Glezer et al., 2015; Binder et al., 2006; Dehaene et al., 2002), we used pseudo-word stimuli to minimize top-down semantic influences. Both real words and pseudowords have an orthographic structure; however, pseudowords do not have meaning that could trigger top-down semantic input (e.g., Kherif, Josse, & Price, 2011) and are thus more suitable for the study of orthographic processing. We created pseudowords using the SUBTLEX database of Polish word frequencies based on 101 million words from film and television subtitles (Mandera, Keuleers, Wodniecka, & Brysbaert, 2015). First, 128 high-frequency (>5 times per million) four-letter words were selected. Next, we selected matching pseudowords with the same frequency of letter bigrams, trigrams, and quadrigrams, thus ensuring that the pseudowords' orthographic structure would be familiar to participants as the structure of frequently occurring words. These pseudowords served as target and prime stimuli (Figure 1A). Half of the target pseudowords had a two-dot letter (in Polish braille, this includes

Table 1. Participant Characteristics

<i>Participant</i>	<i>Age (years)</i>	<i>Gender</i>	<i>Cause of Blindness</i>	<i>Reading Hand</i>
1	21	Male	Retinopathy of prematurity	Left
2	26	Female	Retinopathy of prematurity	Left
3	19	Male	Atrophy of the optic nerve	Left
4	24	Female	Atrophy of the optic nerve	Right
5	22	Female	Retinopathy of prematurity	Right
6	27	Female	Atrophy of the optic nerve	Right
7	33	Female	Toxoplasmosis	Right
8	19	Female	Retinopathy of prematurity	Right
9	24	Male	Retinopathy of prematurity	Right
10	34	Male	Atrophy of the optic nerve	Left
11	33	Male	Retinopathy of prematurity	Left
12	31	Female	Retinopathy of prematurity	Left
13	20	Male	Atrophy of the optic nerve	Left

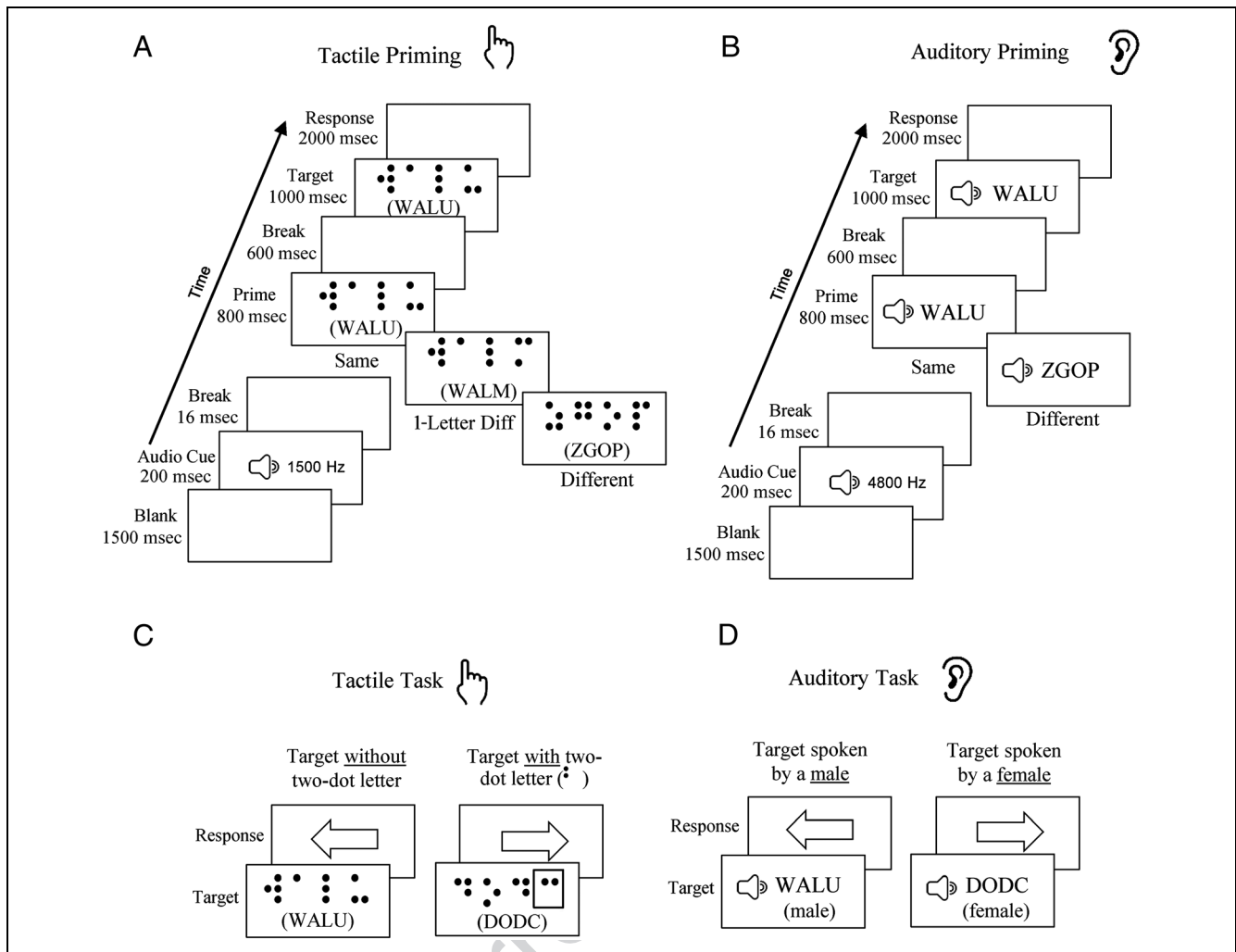


Figure 1. Experimental paradigm. Participants were exposed to prime–target pairs of four-letter pseudowords either in three variants (same, 1-letter different, different) in the tactile modality (A) or in two variants (same, different) in the auditory modality (B). To minimize top–down processing, we used a task that focused on the physical aspect of the task for both modalities (C, D). Participants were asked to discriminate whether the target pseudoword had one of the two-dot braille letters when stimuli were displayed in braille (C) or indicate if the target pseudoword was spoken by a male or a female voice (D).

the letters a, b, c, e, i, and k) in the final (fourth) letter position. One hundred forty-four prime–target pairs from the obtained set of stimuli (48 same–same pairs, 48 same–1-letter different pairs, and 48 same–different pairs, 144 total) were used in the behavioral experiment that preceded the fMRI experiment (see below). The remaining 240 prime–target pairs were used in the fMRI experiment. All prime–target pairs were presented both in braille and in the auditory modality (see Experimental Design and Task section below). Finally, an additional condition [prime–target pairs of real braille words (“same,” “different”)] was also included to be used as an independent functional localizer for ROI analysis.

Behavioral Testing

First, we carried out the experiment outside the scanner to familiarize the participants with the experimental task.

They performed the same discrimination task as the one later used in the fMRI experiment, but with a separate set of stimuli (see Stimuli section). In priming paradigms, the participants’ conscious attention to primes is not necessary for the priming effect to occur (e.g., Dehaene et al., 2001; Naccache & Dehaene, 2001); nevertheless, we tested in several ways that the participants were actually able to read all four letters in the pseudoword primes and targets in the allotted time. Thus, during behavioral testing, we measured the trajectory of reading finger movement using the finger-tracking system developed by Aranyanak and Reilly (2013). All participants read the prime and target stimuli in full, from the first to the last letter, in the allotted time. Moreover, in five participants, we ran an additional test during which the participants were presented with a list of 20 pseudowords and 20 words: Half of the stimuli occurred in the behavioral experiment and half did not. They were then asked to

evaluate whether the presented stimuli had occurred in the experiment. In this test, participants correctly recognized 85% ($SD = 0.98$) of the stimuli.

Experimental Design and Task— General Description

All stimuli were presented using Presentation software (<https://www.neurobs.com/>). Tactile stimuli were displayed on the BraillePen 12 Touch (www.harpo.com.pl) in the behavioral experiment and on an fMRI-compatible braille display (Neurodevice, Warsaw, Poland; see Debowska, Wolak, Soluch, Orzechowski, & Kossut, 2013) during the fMRI experiment. This braille display operates similarly to commercial braille devices, has pneumatically driven braille pins, and can display up to five braille characters that can be read in a manner identical to regular braille text, that is, by swiping ones' finger across them. The braille display was placed on participants' thighs (on the reading hand side). Auditory stimuli were recorded by a female and a male speaker and presented on a pair of headphones (in the fMRI: EarPlug, NordicNeuroLab, Bergen, Norway). In each fMRI run, auditory and tactile stimuli were presented together throughout the run in a pseudorandom order. Before each trial, participants were cued, with an audio beep of either 4800 or 1500 Hz (200-msec duration) whether a tactile or an auditory trial was about to begin (see Experimental Design and Task—Trial Description section below; Figure 1A, B).

The following design was used both in the behavioral testing and in the fMRI experiment itself. Prime–target pseudoword pairs were presented both in braille (“same,” “1-letter different,” “different” conditions; see Figure 1A) and in the auditory modality (“same,” “different”; see Figure 1B) in the priming paradigm. Our primary objective was to test whether we could find tactile orthographic priming in the vOT of the blind. To test this hypothesis with more rigor, we included all three conditions used in previous studies of orthographic priming in the sighted (Glezer et al., 2009, 2015), including the 1-letter different condition. Our secondary objective was to compare priming effects in auditory and tactile modalities. Because in this objective we simply wanted to determine either the existence or absence of priming, only the two basic conditions (same and different) were used in the auditory modality. This choice was also dictated by the necessity to include a sufficient number of trial repetitions required in fMRI priming paradigms (each main condition was repeated 80 times across the whole experiment, i.e., across all five fMRI runs) and by the long duration ($t = 62.5$ min) of the experiment.

Participants were thus exposed to prime–target pairs of four-letter pseudowords either in three variants (same, 1-letter different, different) in the tactile modality (Figure 1A) or in two variants (same, different) in the

auditory modality (Figure 1B). To minimize top–down processing, for both the tactile and the auditory modalities we used tasks that focused on the physical aspect of the stimulus (following Mano et al., 2013; Vinckier et al., 2007; Binder et al., 2006). Although it was not possible to use the same task, as the physical aspects of the tactile and auditory words are obviously different, we nonetheless strived, as far as possible, to use two tasks that did not consciously engage the high-level semantic and phonological representations (an example of such a task would be categorization or reading aloud). Thus, for braille, participants were asked to discriminate whether the target pseudoword had one of the two-dot braille letters (Figure 1C); for auditory stimuli, they were asked to indicate whether the target pseudoword was spoken by a male or a female voice (Figure 1D). In both cases, participants had to respond by pressing one of the two corresponding response keys. Participants performed the same task in both the behavioral and fMRI experiments, but with two different sets of stimuli to avoid the repetition effect.

Experimental Design and Task—fMRI Design and Trial Description

In the fMRI experiment, we used an event-related design. The experiment had five runs. In each run, 80 trials were presented at a rate of one trial every 6100 msec. Each trial began with an auditory cue (200-msec beep), indicating either a tactile trial (1500 Hz) or an auditory trial (4800 Hz), followed by a 16-msec blank. Then, a prime was presented for 800 msec, followed by a 600-msec blank, a 1000-msec target, 2000-msec RT, and an additional 1500-msec blank (Figure 1). To introduce the necessary jitter in the event-related paradigm, in each run we additionally presented additional 16 “blank trials,” during which nothing was either heard or displayed on the braille stimulator for the entire 6100 msec (identical to the length of the trial), similar to the study of Glezer et al. (2009, 2015). Finally, a reduced number of trials containing tactile real words pairs (six per run) was introduced as an additional localizer for ROI analysis. In each run, auditory and tactile stimuli were presented together across the run in a pseudorandom order. To control for long-lag priming effects (Henson, Shallice, & Dolan, 2000), each participant was presented with one prime–target pseudoword pair only twice in the whole experiment (once in the tactile and once in the auditory modality in a counterbalanced order). The same participants also performed a second experiment on braille reading, the results of which were used for ROI definition (see second paragraph of fMRI Data Analysis section, below).

fMRI Acquisition

All fMRI data were acquired at Małopolskie Centrum Biotechnologii in Kraków. fMRI scans were collected

using an EPI sequence on a 3-T Siemens Skyra scanner. A 64-channel head coil was used (flip angle = 90°, repetition time = 1500 msec, echo time = 53 msec, field of view = 192 mm, 64 × 64 matrix). Twenty-eight interleaved axial slices (thickness = 3.5 mm, in-plane resolution = 3.0 × 3.0 mm²) were acquired. 3-D T1-weighted MPRAGE images (resolution 1 × 1 × 1 mm³) were also acquired for each participant.

fMRI Data Analysis

All fMRI data were analyzed using the SPM12 software package. (www.fil.ion.ucl.ac.uk/spm/software/spm12/). A standard preprocessing pipeline was used in which all the acquired functional volumes were corrected to the first slice for EPI distortion and slice acquisition time; they were subsequently realigned using rigid body transformations to correct for head movements, normalized to the standard adult template (Montreal Neurological Institute [MNI] space), and smoothed with an 8-mm (FWHM) Gaussian kernel. The hemodynamic activity for each condition (tactile: same, 1-letter different, different, real words; auditory: same, different) and six estimated movement parameters as regressors were first modeled within a general linear model for each participant. In the second-level analysis, we carried out a random-effects ANOVA.

For the ROI analysis, two ROI definition methods were available to us. The first definition method was based on the word stimuli that were included in the main experiment (words–rest contrast). The second method was based on data from another experiment on braille reading performed by the same participants (Raczy et al., 2016, Poster at the 8th Annual Meeting of the Society for the Neurobiology of Language, for the full description please see Supplemental Materials). In this experiment, participants read five-letter strings of varying approximation to Polish orthography (five conditions of five-letter strings with increasing similarity to real words: from infrequent letter strings such as “gcyzm” to pseudowords like “zotym”; Raczy et al., 2016, Poster at the 8th Annual Meeting of the Society for the Neurobiology of Language) displayed on the same braille display. In this method, we used the All Tactile Strings (all five tactile conditions) versus Nonsense Braille (strings of six-dot braille signs) contrast. Both methods yielded similar results. Here (Figure 3A, B), we present data from ROIs based on the second method.

When defining ROIs we identified, in each participant, 30 voxels that were the most active within the anatomically defined boundaries of a given region (noncontiguous voxels). For the vOT ROI, the search for activated voxels was constrained by a box with anatomical boundaries ($z_{\max} = -10$, $z_{\min} = -25$, $y_{\min} = -70$, $y_{\max} = -40$, $x_{\min} = -60$, $x_{\max} = -30$) that was large enough to encompass the activations previously published in the literature (for the VWFA approximate Talairach coordinates $-43 -54 -12$; see Szwed, Qiao, Jobert, Dehaene, & Cohen, 2014; Reich et al., 2011; Szwed et al., 2011;

Cohen & Dehaene, 2004) We then used these voxels to extract beta activation parameters for each participant in all experimental conditions of interest. The average location of the vOT ROIs was MNI: $-43 \pm 8 -57 \pm 7 -18 \pm 3$ (mean \pm SD). For the individual locations of the vOT ROI for each participant, please see Supplemental Table 2. Using in-house MATLAB code, the activations were averaged first across all 30 voxels and then across participants for each condition and entered into a repeated-measures ANOVA. The activation values (regression coefficient estimates) reported in ROI plots (Figure 3A, B) are shown in arbitrary units (beta) proportional to BOLD activation percentage. For the STS ROI, the same procedure was applied, but with the difference that anatomical boundaries were selected based on locations previously reported in the literature (Vaden et al., 2010; Arnaud et al., 2013, with approximate Talairach coordinates $-63, -30, 3 \pm 10$; STS anatomical boundaries: $z_{\max} = 15$, $z_{\min} = 0$, $y_{\min} = -45$, $y_{\max} = -30$, $x_{\min} = -80$, $x_{\max} = -55$). The average location of the STS ROIs was MNI: $-63 \pm 4 -37 \pm 2 7 \pm 3$ (mean \pm SD). For the individual locations of the STS ROI for each participant, please see Supplemental Table 3.

In the second-level whole-brain analysis, we carried out a random-effects ANOVA analysis for the group. Because the repetition suppression is constrained to the unique population of neurons that respond to certain stimuli and its effects are relatively weak (see Barron, Garvert, & Behrens, 2016, for a general discussion) in all contrasts, unless otherwise stated, we applied a relatively lenient threshold of $p < .002$ voxel wise, $p < .05$ cluster wise ($k = 80$ voxels, uncorrected), similar to other repetition studies (e.g., Glezer et al., 2009, 2015; Devlin, Jamison, Matthews, & Gonnerman, 2004; Dehaene et al., 2001).

RESULTS

Braille Reading Speed Tests

The mean tactile reading speed among the participants in the single word reading test (Konopnicki test) was 60.5 words per minute ($SD = 19.80$, range = 33–93). The reading speed of the text with full sentences (“Farsa Pani Heni”) was 45 words per minute ($SD = 16.13$, range = 20–69). The mean accuracy of the answers in the multiple-choice questionnaire concerning the text was 85% ($SD = 0.09$). Although no braille reading speed norms exist for Polish, these results indicate that all participants were fluent braille readers, especially when considering the fact that, unlike English braille, Polish braille does not use abbreviations and is thus slower to read.

Behavioral Experiment

Before performing the experiment in the MRI scanner, participants performed the same paradigm offline

outside the scanner. Besides familiarizing the participants with the task, the aim of this preliminary experiment was to test for behavioral priming effects. The participants' accuracy in the discrimination task (in which participants had to decide whether there was a two-dot letter within a target pseudoword) was 91% ($SD = 0.7$). The behavioral data were analyzed to determine whether blind participants would show behavioral priming effects for RTs that were similar to those observed in the sighted (e.g., Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2007; Devlin et al., 2004; Dehaene et al., 2001; Giraudo & Grainger, 2001). A repeated-measures ANOVA was used to test for effect between three experimental conditions (same, 1-letter different, different) in the tactile modality: significant, $F(2, 24) = 11.966, p < .001$. Post hoc analyses indicated that the significant effect was due to the difference between same and different conditions, between 1-letter different and different, and between same and 1-letter different ($p = .001, p = .019$, and $p = .030$, respectively). We also performed a paired t test for two experimental conditions (same, different) in the auditory modality; this revealed a significant difference between conditions ($p < .001$). The accuracy of the performance in the auditory task was 90% ($SD = 0.1$). We also tested for a potential accuracy difference between auditory and tactile conditions and found no significant difference (t test, $p = .345$).

Behavior in the Scanner

During the fMRI experiment, the participants performed the same discrimination task as described above. Behavioral data from the scanner replicates the previously found priming effect on RTs in the tactile modality, $F(2, 24) = 29.780, p < .001$, with significant differences between all three conditions in the tactile modality (t test, all $ps < .005$). A paired t test for two experimental conditions (same, different) in the auditory modality also replicates a significant difference between conditions

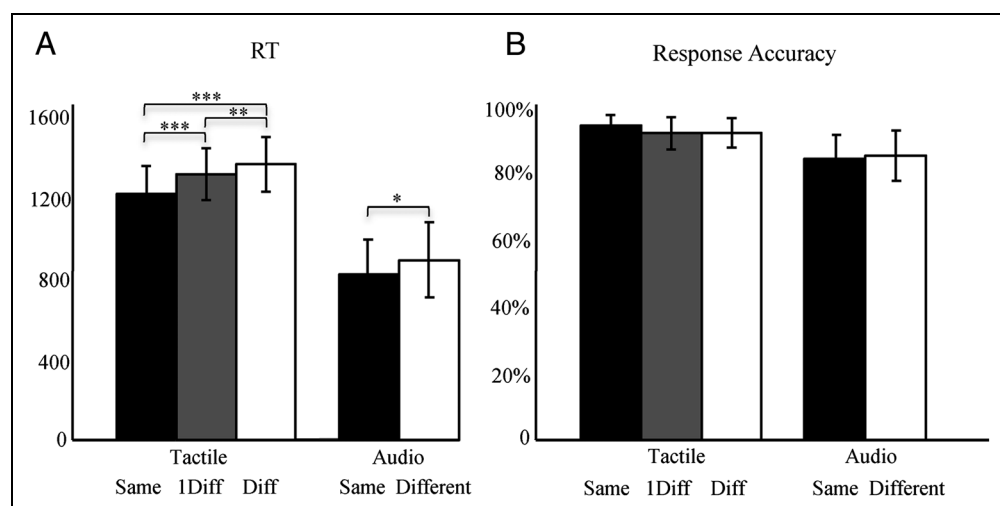
($p = .023$; Figure 2A). Mean performance accuracy for the tactile conditions was 94% ($SD = 0.05$; Figure 2B), and mean performance accuracy for auditory conditions was 85% ($SD = 0.17$, Figure 2B; difference between conditions significant, t test, $p = .009$).

ROI Analysis

Our a priori hypotheses were based on existing literature (Glezer et al., 2009, 2015; Arnaud et al., 2013; Vaden et al., 2010) and predicted that differences between conditions of interest would be small and limited to specific brain regions. The key analysis was therefore an ROI analysis performed in the left vOT and STS. (Figure 3A, B). For the tactile stimuli, the left vOT showed significant differences in activation between all three experimental conditions (same, 1-letter different, different), ANOVA, $F(2, 24) = 6.567, p = .005$. Significant differences in activation were found between the different condition and both 1-letter different and same conditions (t test, $p = .029$ and $p = .006$, respectively) and between 1-letter different and same conditions (t test, $p = .027$, all values uncorrected; Figure 3A). The same result was found when activations from the right vOT of the two right-lateralized participants (see Methods section) were added to the analysis (significant differences in activation between all three experimental conditions: same, 1-letter different, different, ANOVA, $F(2, 28) = 6.521, p = .005$). Similar results were also obtained with an alternative ROI definition, that is, with an ROI based on a real braille words pairs condition versus rest.

The activations for auditory stimuli were threefold weaker activations than for tactile stimuli (Figure 3A). We found no significant difference between two auditory conditions (different vs. same) in the vOT ROI (t test, $p = .11$; Figure 3A), similar to results reported previously for the vOT in the sighted for the type of task used here (Cohen et al., 2004; Dehaene et al., 2002). Then, because repetition suppression for auditory stimuli can be

Figure 2. Behavioral results in the scanner. RTs (A) and response accuracy (B) in both modalities (tactile and auditory). Significance levels: *** $p < .001$, ** $p < .01$, * $p < .05$. A significant difference was found between tactile and auditory modalities for both RT and accuracy ($p < .01$) with no between-condition differences in response accuracy (all $ps > .1$).



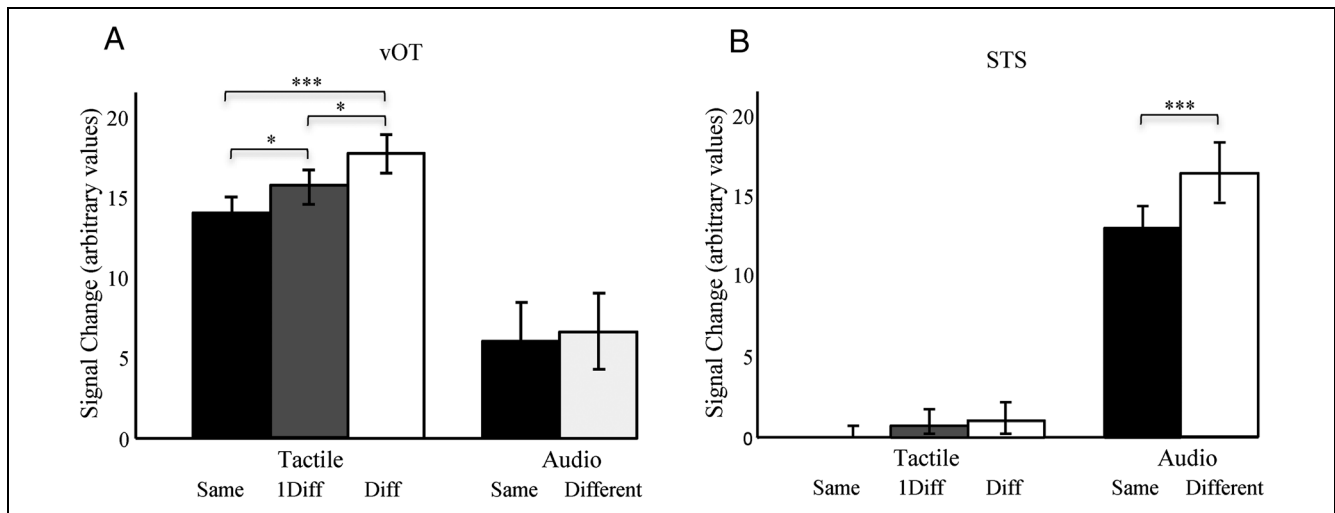


Figure 3. ROI analysis. Signal change in the vOT (A) and the STS (B) in three experimental conditions (same, 1-letter different, different) in tactile modality and in two experimental conditions (same, different) in auditory modality is shown. A three-way ANOVA with the condition (same/different), modality (auditory/tactile), and site (vOT/STS) as factors and participants as random factor revealed a significant trend of modality, $F(1, 84) = 3.67, p = .059$, an effect of site, $F(1, 84) = 4.55, p = .036$, and, most notably, an interaction of Modality \times Site, $F(1, 84) = 64.62, p < .001$, indicating a very significant difference between the vOT and the STS in their responses to stimuli from these two modalities. Significance levels: *** $p < .005$, ** $p < .01$, * $p < .05$.

observed in the STS in both sighted participants (Vaden et al., 2010; Cohen et al., 2004; Dehaene et al., 2002) and blind participants (e.g., Arnaud et al., 2013), we performed an ROI analysis in the left STS (Figure 3B). It showed a significant difference between the two auditory conditions (different vs. same, $p < .001$, t test). No significant differences between the three tactile conditions (different, 1-letter different, same) were found in the STS, $F(2, 24) = 2.162, p = .137$ (Figure 3B).

Finally, to directly test for a double spatial dissociation between the vOT and the STS, we compared the activation profiles in the vOT and the STS with a three-way ANOVA with the condition (same/different), modality (auditory/tactile), and site (vOT/STS) as factors and participants as a random factor. This ANOVA revealed a trend of modality, $F(1, 84) = 3.67, p = .059$, an effect of site, $F(1, 84) = 4.55, p = .036$, and, most notably, an interaction of Modality \times Site, $F(1, 84) = 64.62, p < .001$,

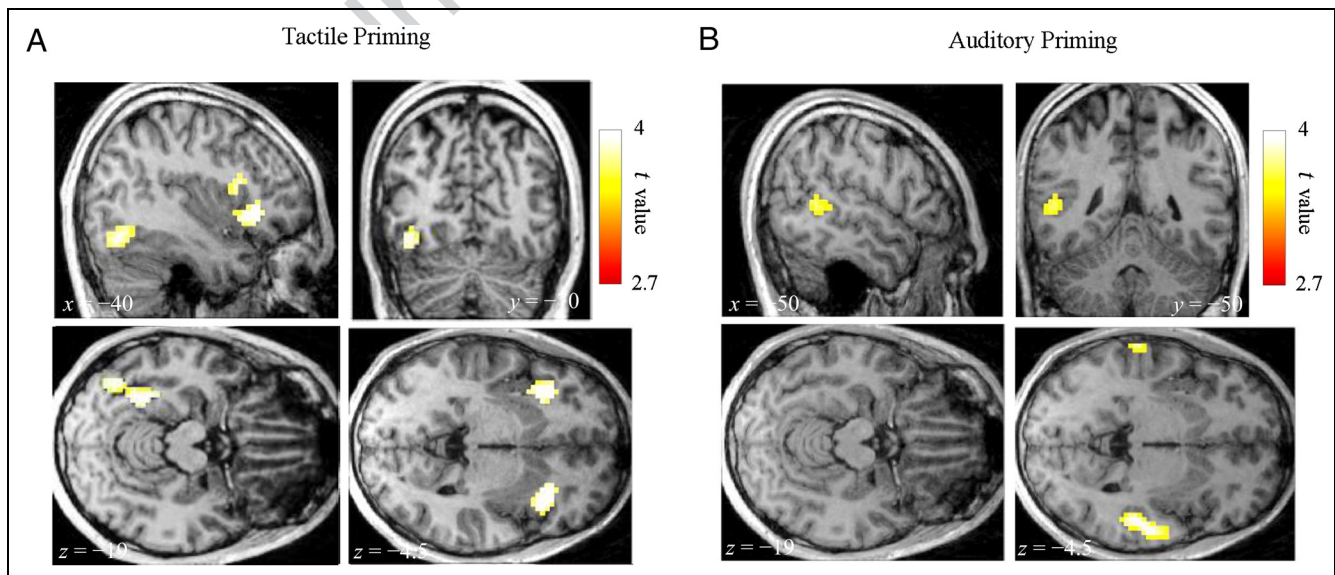


Figure 4. Results from whole-brain analyses for the different versus same conditions for (A) the tactile stimuli and (B) the auditory stimuli. Threshold in (A) $p < .002$ voxel-wise, (B) $p < .005$ voxel-wise, cluster-wise threshold (A, B): $k = 80$ voxels.

which indicates a very significant difference between the vOT and the STS in their responses to stimuli from these two modalities.

Whole-brain fMRI Analysis

To probe for additional repetition suppression effects across the brain, we also conducted whole-brain analyses. We first compared activations induced by different versus same conditions in the tactile modality (Figure 4A). This contrast revealed an activation in the left vOT that is consistent with the ROI results (peak MNI = -33, -55, -19, $t = 3.95$, cluster size $k = 83$ voxels, cluster level $p = .050$). Additional activations were also found in the left (peak MNI = -36, 20, -1, $t = 4.01$, cluster size $k = 188$ voxels, cluster level $p = .006$) and right (peak MNI = 30, 20, 10, $t = 4.35$, cluster size $k = 231$ voxels, cluster level $p = .003$) inferior frontal gyrus, bilaterally in the insula (peak MNI = 12, 14, 48, $t = 4.25$, cluster size $k = 228$ voxels, cluster level $p = .003$) and in the primary visual cortex (peak MNI = -24, -97, 17, $t = 4.00$, cluster size $k = 118$ voxels, cluster level $p = .022$). Next, we compared the activations induced by 1-letter different versus same conditions and different versus 1-letter different conditions in tactile modality, but we failed to obtain a significant activation for those contrasts in the whole-brain analysis. Second, we compared the activations induced by different versus same condition in the auditory modality (Figure 4B). As expected, it revealed a significant activation in the right STS (peak MNI = 51, -37, -1, $t = 4.47$, cluster size $k = 100$ voxels). An activation in the left STS was found only at a lower threshold of $p < .005$ voxel-wise (peak MNI = -66, -28, -1, $t = 4.18$, cluster size $k = 88$ voxels). A conjunction analysis (same vs. different tactile \cap same vs. different auditory) revealed no significant voxels even at an exploratory threshold of $p = .01$ voxel-wise, uncorrected.

DISCUSSION

In this study, we found a double dissociation between tactile orthographic repetition suppression in the left vOT and auditory repetition suppression in the left STS. When presented with tactile stimuli, the vOT of the blind showed a repetition suppression effect that has been observed in the VWFA of the sighted for visual pseudowords (Glezer et al., 2009, 2015). This orthographic priming effect in vOT was found only for the tactile modality. VOT responses to auditory stimuli were weaker, and as consistent with previous results (Cohen et al., 2004; Dehaene et al., 2002), we found no repetition suppression effects for spoken letter strings. Conversely, the STS of the blind exhibited repetition suppression for spoken letter strings, but not for braille letter strings.

fMRI orthographic repetition suppression has been studied previously in the sighted, notably by Glezer et al. (2009, 2015), on whose work our experiment is

based, by Cohen et al. (2004), Dehaene et al. (2001, 2002), Devlin et al. (2004) and Wimmer, Ludersdorfer, Richlan, and Kronbichler (2016). Orthographic repetition suppression in the VWFA for written stimuli was consistently observed in all of the above experiments. Our study demonstrates orthographic repetition suppression for braille pseudowords in the vOT of the blind. This indicates that neurons in the vOT can make discriminations between small changes among two novel tactile stimuli, braille pseudowords, made out of highly trained parts, braille letters. In our opinion, this constitutes evidence for the vOT's sensitivity to frequently occurring combinations of tactile information, that is, letters and thus to sublexical orthographic structure of braille stimuli, and consequently its importance in tactile reading. Repetition suppression for auditory pseudowords, but not tactile ones, was observed in the STS, similar to Arnaud et al. (2013) in the blind and Vaden et al. (2010) and Arnaud et al. (2013) in the sighted. The latter result is consistent with the function of the STS as a hub region for phonological processing (reviewed in DeWitt & Rauschecker, 2012; Hickok & Poeppel, 2004). Indeed, whole-brain analysis (Figure 4) confirmed our assumptions that the most significant priming effects for the auditory modality would be found in the STS.

As mentioned in the introduction, the task-specific principle is supported by a large body of data from sensory-deprived and nondeprived participants (Bola, Zimmermann, et al., 2017; Sigalov, Maidenbaum, & Amedi, 2016; Siuda-Krzywicka et al., 2016; Heimler, Weisz, & Collignon, 2014; Striem-Amit, Cohen, Dehaene, & Amedi, 2012; Reich et al., 2011; Renier et al., 2010; Amedi et al., 2001, 2007; Poirier et al., 2006; Pascual-Leone & Hamilton, 2001) and by animal data (e.g., Lomber, Meredith, & Kral, 2011). These data, however, must be reconciled with data from blind participants, which show that the deprived brain is also pluripotent and the task-selective principle does not always apply. The latter results indicate that the visual cortex of the blind becomes a high-level cognitive region involved in tasks such as memory and language processing and numerical processing (Kanjlia et al., 2016; Bedny, Richardson, & Saxe, 2015; Lane et al., 2015; Bedny et al., 2011; Amedi et al., 2003, 2004). Animal studies (e.g., Sharma, Angelucci, & Sur, 2000) also show considerable pluripotentiality in the deprived cortex. The question then becomes how general the task-specific principle is and in which particular cases it does or does not apply.

Our results indicate that, in the particular case of tactile reading in the blind, the task-specific principle does apply to a significant extent. Admittedly, it can be inferred from other studies that the selectivity of vOT to tactile reading is smaller than its selectivity for visual reading in the sighted (Reich et al., 2011). Several studies in the sighted show stronger MRI vOT responses to written stimuli compared with objects (Mano et al., 2013; Szwed et al., 2011; Kanwisher, 2010; Baker et al., 2007) and

stronger intracranial EEG responses to written stimuli compared with objects and faces (Perrone-Bertolotti et al., 2014; Hamamé et al., 2013; Nobre et al., 1994). In the blind, vOT responses to braille words are very similar to activations elicited by verb generation—stimuli that do not evoke significant responses in the vOT of the sighted (Burton, Snyder, Diamond, & Raichle, 2002; Reich et al., 2011). Nonetheless, here we found that the vOT of the blind displayed orthographic repetition suppression for braille pseudowords, a hallmark of orthographic processing (Glezer et al., 2009, 2015) indicating that this brain region is indeed sensitive to frequently occurring combinations of tactile letters and thus to the sublexical orthographic structure of braille stimuli. This result suggests that task-specific brain reorganization applies at least partially in the case of reading mechanisms in the congenitally blind brain. Our conclusion is also supported by recent data from blind participants, which indicates that the recruitment of dorsal occipital regions during mathematical cognition in the blind relates to the intrinsic computational role of these regions in auditory spatial processing (Crollen et al., 2019).

A whole-brain analysis that sought to find out the extent of the vOT effect as well as additional regions that might exhibit repetition suppression revealed an effect for tactile braille in the left vOT. This effect had two peaks: a more lateral peak (MNI $-39 -70 -19$) and a more medial peak (MNI $= -33, -55, -19$). Both peaks, especially the second one, were located more slightly medially than the typical VWFA in the sighted. A repetition suppression effect for tactile stimuli was also revealed in the primary visual cortex (MNI $= -24, -97, 17$). We believe that these observations should be considered in the light of the fact that the visual cortex of the blind becomes involved in general language processing (Bedny, 2017; Amedi et al., 2003), which might affect the location and function of the reading area. Indeed, work on the connectivity of the sighted VWFA by Bouhali and colleagues (2014) indicates that the connectivity of the VWFA to language areas may be the primary determinant of its localization. Based on Bouhali and colleagues (2014), we speculate that if the vOT of the blind indeed had an important role in reading, its location would be altered by the connectivity to additional language areas in the blind that are situated in the visual cortex. Data from sighted participants who have learnt to read braille show that tactile information reaches the visual system through cortico-cortical connections between somatosensory areas and early visual areas (Bola, Siuda-Krzywicka, et al., 2017). In the blind, tactile information might also reach early visual areas through the lateral geniculate nucleus, which, in the blind, becomes “invaded” by tactile input (Reislev et al., 2017). We therefore hypothesize the primary visual cortex of the blind might constitute a “second braille word form area,” tasked, perhaps, with more basic steps of braille word recognition, for example, letter recognition. A clinical

case study of an early-blind woman, once highly proficient at reading braille but later rendered unable to do so following a bilateral occipital stroke, supports the notion of a causal relationship between the ability to read braille and the function of occipital areas (Hamilton, Keenan, Catala, & Pascual-Leone, 2000). Finally, an additional activation in the whole-brain analysis was found in the left and right inferior frontal gyri and most likely reflected task-related processes that are facilitated by identity priming.

Our results also touch upon a more general question: A long line of research has investigated how multifunctional ventral visual areas can be. On one hand, the ventral visual cortex comprises the fusiform face area, the most specialized sensory area ever described (e.g., Schalk et al., 2017; Tsao & Livingstone, 2008; Kanwisher & Yovel, 2006; Kanwisher, McDermott, & Chun, 1997), containing neurons that respond exclusively to faces (Tsao, Freiwald, Tootell, & Livingstone, 2006). On the other hand, the face area seems to be an exception as research—notably research on the relationship between visual object recognition and visual word recognition—suggests that the same area can subserve both object and visual word recognition (e.g., Szwed et al., 2011). The VWFA develops in a region originally engaged in object recognition (e.g., Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Szwed et al., 2011; Dehaene et al., 2010), and sensitivity to letter strings emerges gradually during development (Brem et al., 2010). Although the conversion from object to word recognition can be profound and intracranial recordings reveal small clusters of neurons that respond exclusively to words but not to objects (Perrone-Bertolotti et al., 2014; Hamamé et al., 2013; Nobre et al., 1994), most neurons in the VWFA also show considerable responses to objects (see, e.g., Mano et al., 2013; Figure 4 in Szwed et al., 2011; or Figure e-2 in Hamamé et al., 2013). Indeed fMRI results show that in tasks such as the naming task, the entire sighted VWFA might show stronger responses to objects than to words (e.g., Mechelli, Josephs, Lambon Ralph, McClelland, & Price, 2007). Results from sighted participants thus show that visual word recognition is performed by an area engaged in recognition of other object categories. Furthermore, our knowledge of other cortical areas, for example, of the parietal cortex, indicates that the same brain region can perform not only one function (recognition) on many stimulus classes (words and objects) but several different functions such as spatial attention, categorical, and associative processes (reviewed in Fitzgerald, Swaminathan, & Freedman, 2012). It is not implausible then that, in the vOT of the blind, tactile word recognition can coexist with other functions specific to the blind visual cortex, namely working memory and general language processing.

In the sighted, repetition suppression demonstrates that words show tighter tuning (i.e., a release from suppression occurs already when one of the words’

constituent letter is changed and almost no repetition suppression occurs for 1-letter difference between prime and target) than pseudowords (where release from suppression is gradual and substantial repetition suppression still occurs for 1-letter difference between prime and target). According to Glezer and colleagues (2009), this indicates that the VWFA contains neurons tightly tuned to entire words. Our results establish that the blind participants' vOT exhibits repetition suppression to pseudowords in the tactile modality, indicating that it is sensitive to learned combinations of tactile letters, that is, to the sublexical orthographic structure of braille stimuli. Further research should demonstrate whether vOT in the blind would also show tighter tuning to the whole words.

The limitations of this study stem primarily from comparing neural activation across modalities and across tasks that focused on the physical aspects of the stimuli. These aspects and tasks are inevitably particular to their specific modalities (tactile, auditory, etc.). It could be possible that the differences between the letter detection task in the tactile modality and the gender detection task in the auditory modality might have influenced the results to some degree. These differences are manifested in varying RTs (1342 msec for tactile vs. 889 msec for auditory stimuli) and a difference in performance rate (tactile: 94% vs. auditory: 85%). Although the detection of two-dot letters might arguably induce a top-down attentional focus on fine-grained low-level tactile differences, which is not present in the voice gender detection task performed in the auditory domain, such a focus should, if anything, reduce orthographic priming effects for the tactile condition. In fact, a similar task (detecting letters with ascenders such as “d,” “t,” and “b” and descenders such as “q” or “j”) is commonly used in research on visual reading (Binder et al., 2006), including studies using the repetition suppression technique (Nakamura et al., 2012; Pegado, Nakamura, Cohen, & Dehaene, 2011), precisely to ensure that the orthographic processing itself is carried out in an implicit and automatic manner. Also, the general pattern of our results is consistent with previous data obtained in other tasks. Stronger vOT responses for tactile versus auditory stimuli are reported by, for example, Kim et al. (2017), who used a memory probe task. Thus, it is very unlikely that a change in the task used or a change in the task difficulty could have had affected the main finding presented here, namely the existence of orthographic priming in the vOT for tactile pseudowords, but not for auditory pseudowords.

In conclusion, our results reveal a double dissociation, with tactile orthographic priming in the vOT and auditory orthographic priming in the STS, a general language area. Reconciling our findings of orthographic priming in the vOT of the blind, with evidence showing acquisition of new high-level functions in that region, we propose that the vOT in the blind serves multiple functions, some of which overlap to some extent with the function of the

VWFA in the sighted. This view accommodates both task-specific reorganization and pluripotential acquisition of new capacities.

Acknowledgments

This work was supported by the Polish National Science Centre (Grant Number 2015/19/B/HS6/01256) to M. S. We would like to thank all our participants for their effort and for participating in the study, Katarzyna Jednoróg for helpful comments, Michael Timberlake for language editing, and Paweł Hańczur for developing the finger-tracking setup. We would like to acknowledge the Institute for the Blind and Partially Sighted Children in Kraków for organizational help. We thank the Małopolskie Centrum Biotechnologii for technical assistance during collecting the MRI data and Karolina Dukała for administrative assistance.

Reprint requests should be sent to Katarzyna Rączy, Department of Psychology, Jagiellonian University, Ingardena 6, 30-060, Krakow, Poland, or via e-mail: raczy.katarzyna@gmail.com, or Marcin Szwed, Department of Psychology, Jagiellonian University, Ingardena 6, 30-060, Krakow, Poland, or via e-mail: mfszwed@gmail.com.

REFERENCES

- Abboud, S., Maidenbaum, S., Dehaene, S., & Amedi, A. (2015). A number-form area in the blind. *Nature Communications*, 6, 6026.
- Amedi, A., Floel, A., Knecht, S., Zohary, E., & Cohen, L. G. (2004). Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nature Neuroscience*, 7, 1266–1270.
- Amedi, A., Hofstetter, S., Maidenbaum, S., & Heimler, B. (2017). Task selectivity as a comprehensive principle for brain organization. *Trends in Cognitive Sciences*, 21, 307–310.
- Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience*, 4, 324–330.
- Amedi, A., Raz, N., Pianka, P., Malach, R., & Zohary, E. (2003). Early “visual” cortex activation correlates with superior verbal memory performance in the blind. *Nature Neuroscience*, 6, 758–766.
- Amedi, A., Stern, W. M., Camprodon, J. A., Bermpohl, F., Merabet, L., Rotman, S., et al. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. *Nature Neuroscience*, 10, 687–689.
- Aranyan, I., & Reilly, R. G. (2013). A system for tracking braille readers using a Wii remote and a refreshable braille display. *Behavior Research Methods*, 45, 216–228.
- Arnaud, L., Sato, M., Ménard, L., & Gracco, V. L. (2013). Repetition suppression for speech processing in the associative occipital and parietal cortex of congenitally blind adults. *PLoS One*, 8, e64553.
- Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, 104, 9087–9092.
- Barron, H. C., Garvert, M. M., & Behrens, T. E. J. (2016). Repetition suppression: A means to index neural representations using BOLD? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 371, 20150355.

- Bedny, M. (2017). Evidence from blindness for a cognitively pluripotent cortex. *Trends in Cognitive Sciences*, 21, 637–648.
- Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., & Saxe, R. (2011). Language processing in the occipital cortex of congenitally blind adults. *Proceedings of the National Academy of Sciences, U.S.A.*, 108, 4429–4434.
- Bedny, M., Richardson, H., & Saxe, R. (2015). “Visual” cortex responds to spoken language in blind children. *Journal of Neuroscience*, 35, 11674–11681.
- Beisteiner, R., Windischberger, C., Geißler, A., Gartus, A., Uhl, F., Moser, E., et al. (2015). fMRI correlates of different components of braille reading by the blind. *Neurology, Psychiatry and Brain Research*, 21, 137–145.
- Benetti, S., van Ackeren, M. J., Rabini, G., Zonca, J., Foa, V., Baruffaldi, F., et al. (2017). Functional selectivity for face processing in the temporal voice area of early deaf individuals. *Proceedings of the National Academy of Sciences, U.S.A.*, 114, E6437–E6446.
- Binder, J. R., Medler, D. A., Westbury, C. F., Liebenthal, E., & Buchanan, L. (2006). Tuning of the human left fusiform gyrus to sublexical orthographic structure. *Neuroimage*, 33, 739–748.
- Bola, Ł., Siuda-Krzywicka, K., Paplińska, M., Sumera, E., Hańczur, P., & Szwed, M. (2016). Braille in the sighted: Teaching tactile reading to sighted adults. *PLoS One*, 11, e0155394.
- Bola, Ł., Siuda-Krzywicka, K., Paplińska, M., Sumera, E., Zimmermann, M., Jednoróg, K., et al. (2017). Structural reorganization of the early visual cortex following braille training in sighted adults. *Scientific Reports*, 7, 17448.
- Bola, Ł., Zimmermann, M., Mostowski, P., Jednoróg, K., Marchewka, A., Rutkowski, P., et al. (2017). Task-specific reorganization of the auditory cortex in deaf humans. *Proceedings of the National Academy of Sciences, U.S.A.*, 114, E600–E609.
- Bouhali, F., de Schotten, M. T., Pinel, P., Poupon, C., Mangin, J.-F., Dehaene, S., et al. (2014). Anatomical connections of the visual word form area. *Journal of Neuroscience*, 34, 15402–15414.
- Brem, S., Bach, S., Kucian, K., Kujala, J. V., Guttorm, T. K., Martin, E., et al. (2010). Brain sensitivity to print emerges when children learn letter–speech sound correspondences. *Proceedings of the National Academy of Sciences, U.S.A.*, 107, 7939–7944.
- Büchel, C., Price, C., Frackowiak, R. S. J., & Friston, K. (1998). Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain*, 121, 409–419.
- Burton, H., Sinclair, R. J., & Agato, A. (2012). Recognition memory for braille or spoken words: An fMRI study in early blind. *Brain Research*, 1438, 22–34.
- Burton, H., Snyder, A. Z., Conturo, T. E., Akbudak, E., Ollinger, J. M., & Raichle, M. E. (2002). Adaptive changes in early and late blind: A fMRI study of braille reading. *Journal of Neurophysiology*, 87, 589–607.
- Burton, H., Snyder, A. Z., Diamond, J. B., & Raichle, M. E. (2002). Adaptive changes in early and late blind: A fMRI study of verb generation to heard nouns. *Journal of Neurophysiology*, 88, 3359–3371.
- Cai, Q., Lavidor, M., Brysbaert, M., Paulignan, Y., & Nazir, T. A. (2008). Cerebral lateralization of frontal lobe language processes and lateralization of the posterior visual word processing system. *Journal of Cognitive Neuroscience*, 20, 672–681.
- Cohen, L., & Dehaene, S. (2004). Specialization within the ventral stream: The case for the visual word form area. *Neuroimage*, 22, 466–476.
- Cohen, L., Jobert, A., Le Bihan, D., & Dehaene, S. (2004). Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *Neuroimage*, 23, 1256–1270.
- Crollen, V., Lazzouni, L., Rezk, M., Bellemare, A., Lepore, F., Noël, M.-P., et al. (2019). Recruitment of the occipital cortex by arithmetic processing follows computational bias in the congenitally blind. *Neuroimage*, 186, 549–556.
- Debowska, W., Wolak, T., Soluch, P., Orzechowski, M., & Kossut, M. (2013). Design and evaluation of an innovative MRI-compatible braille stimulator with high spatial and temporal resolution. *Journal of Neuroscience Methods*, 213, 32–38.
- Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, 15, 254–262.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, 9, 335–341.
- Dehaene, S., Le Clec'h, G., Poline, J.-B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport*, 13, 321–325.
- Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, 4, 752–758.
- Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science*, 330, 1359–1364.
- Dehaene-Lambertz, G., Monzalvo, K., & Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLoS Biology*, 16, e2004103.
- Devlin, J. T., Jamison, H. L., Matthews, P. M., & Gonnerman, L. M. (2004). Morphology and the internal structure of words. *Proceedings of the National Academy of Sciences, U.S.A.*, 101, 14984–14988.
- DeWitt, I., & Rauschecker, J. P. (2012). Phoneme and word recognition in the auditory ventral stream. *Proceedings of the National Academy of Sciences, U.S.A.*, 109, E505–E514.
- Ding, H., Qin, W., Liang, M., Ming, D., Wan, B., Li, Q., et al. (2015). Cross-modal activation of auditory regions during visuo-spatial working memory in early deafness. *Brain*, 138, 2750–2765.
- Fitzgerald, J. K., Swaminathan, S. K., & Freedman, D. J. (2012). Visual categorization and the parietal cortex. *Frontiers in Integrative Neuroscience*, 6, 18.
- Giraudo, H., & Grainger, J. (2001). Priming complex words: Evidence for supralexical representation of morphology. *Psychonomic Bulletin & Review*, 8, 127–131.
- Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the “visual word form area.”. *Neuron*, 62, 199–204.
- Glezer, L. S., Kim, J., Rule, J., Jiang, X., & Riesenhuber, M. (2015). Adding words to the brain’s visual dictionary: Novel word learning selectively sharpens orthographic representations in the VWFA. *Journal of Neuroscience*, 35, 4965–4972.
- Hamamé, C. M., Szwed, M., Sharman, M., Vidal, J. R., Perrone-Bertolotti, M., Kahane, P., et al. (2013). Dejerine’s reading area revisited with intracranial EEG: Selective responses to letter strings. *Neurology*, 80, 602–603.
- Hamilton, R., Keenan, J. P., Catala, M., & Pascual-Leone, A. (2000). Alexia for braille following bilateral occipital stroke in an early blind woman. *NeuroReport*, 11, 237–240.
- Heimler, B., Weisz, N., & Collignon, O. (2014). Revisiting the adaptive and maladaptive effects of crossmodal plasticity. *Neuroscience*, 283, 44–63.

- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, 287, 1269–1272.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92, 67–99.
- Kanjlia, S., Lane, C., Feigenson, L., & Bedny, M. (2016). Absence of visual experience modifies the neural basis of numerical thinking. *Proceedings of the National Academy of Sciences, U.S.A.*, 113, 11172–11177.
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences, U.S.A.*, 107, 11163–11170.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17, 4302–4311.
- Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 361, 2109–2128.
- Karavatos, A., Kaprinis, G., & Tzavaras, A. (1984). Hemispheric specialization for language in the congenitally blind: The influence of the braille system. *Neuropsychologia*, 22, 521–525.
- Kherif, F., Josse, G., & Price, C. J. (2011). Automatic top–down processing explains common left occipito-temporal responses to visual words and objects. *Cerebral Cortex*, 21, 103–114.
- Kim, J. S., Kanjlia, S., Merabet, L. B., & Bedny, M. (2017). Development of the visual word form area requires visual experience: Evidence from blind braille readers. *Journal of Neuroscience*, 37, 11495–11504.
- Lane, C., Kanjlia, S., Omaki, A., & Bedny, M. (2015). “Visual” cortex of congenitally blind adults responds to syntactic movement. *Journal of Neuroscience*, 35, 12859–12868.
- Lane, C., Kanjlia, S., Richardson, H., Fulton, A., Omaki, A., & Bedny, M. (2017). Reduced left lateralization of language in congenitally blind individuals. *Journal of Cognitive Neuroscience*, 29, 65–78.
- Lomber, S. G., Meredith, M. A., & Kral, A. (2011). Adaptive crossmodal plasticity in deaf auditory cortex: Areal and laminar contributions to supranormal vision in the deaf. *Progress in Brain Research*, 191, 251–270.
- Mandera, P., Keuleers, E., Wodniecka, Z., & Brysbaert, M. (2015). Subtlex-pl: Subtitle-based word frequency estimates for Polish. *Behavior Research Methods*, 47, 471–483.
- Mano, Q. R., Humphries, C., Desai, R. H., Seidenberg, M. S., Osmon, D. C., Stengel, B. C., et al. (2013). The role of left occipitotemporal cortex in reading: Reconciling stimulus, task, and lexicality effects. *Cerebral Cortex*, 23, 988–1001.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review*, 88, 375–407.
- Mechelli, A., Josephs, O., Lambon Ralph, M. A., McClelland, J. L., & Price, C. J. (2007). Dissociating stimulus-driven semantic and phonological effect during reading and naming. *Human Brain Mapping*, 28, 205–217.
- Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: The opportunity of change. *Nature Reviews Neuroscience*, 11, 44–52.
- Millar, S. (1997). *Reading by touch*. London: Routledge.
- Naccache, L., & Dehaene, S. (2001). The priming method: Imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cerebral Cortex*, 11, 966–974.
- Nakamura, K., Dehaene, S., Jobert, A., Le Bihan, D., & Kouider, S. (2007). Task-specific change of unconscious neural priming in the cerebral language network. *Proceedings of the National Academy of Sciences, U.S.A.*, 104, 19643–19648.
- Nakamura, K., Kuo, W.-J., Pegado, F., Cohen, L., Tzeng, O. J. L., & Dehaene, S. (2012). Universal brain systems for recognizing word shapes and handwriting gestures during reading. *Proceedings of the National Academy of Sciences, U.S.A.*, 109, 20762–20767.
- Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, 372, 260–263.
- Pascual-Leone, A., & Hamilton, R. (2001). The metamodal organization of the brain. *Progress in Brain Research*, 134, 427–445.
- Pegado, F., Nakamura, K., Cohen, L., & Dehaene, S. (2011). Breaking the symmetry: Mirror discrimination for single letters but not for pictures in the visual word form area. *Neuroimage*, 55, 742–749.
- Perrone-Bertolotti, M., Vidal, J. R., de Palma, L., Hamamé, C. M., Ossandon, T., Kahane, P., et al. (2014). Turning visual shapes into sounds: Early stages of reading acquisition revealed in the ventral occipitotemporal cortex. *Neuroimage*, 90, 298–307.
- Poirier, C., Collignon, O., Scheiber, C., Renier, L., Vanlierde, A., Tranduy, D., et al. (2006). Auditory motion perception activates visual motion areas in early blind subjects. *Neuroimage*, 31, 279–285.
- Price, C. J., & Devlin, J. T. (2011). The Interactive Account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences*, 15, 246–253.
- Raczy, K., Sadowska, A., Boros, M., Chabuda, A., Hańczur, P., Sumera, E., et al. (2016). *There is no “pure” orthographic brain area in the visual system of the blind*. Poster session presented at the SNL Conference, London.
- Reich, L., Szwed, M., Cohen, L., & Amedi, A. (2011). A ventral visual stream reading center independent of visual experience. *Current Biology*, 21, 363–368.
- Reicher, G. M. (1969). Perceptual recognition as a function of meaningfulness of stimulus material. *Journal of Experimental Psychology*, 81, 275–280.
- Reislev, N. H., Dyrby, T. B., Siebner, H. R., Lundell, H., Pito, M., & Kupers, R. (2017). Thalamocortical connectivity and microstructural changes in congenital and late blindness. *Neural Plasticity*, 2017, 9807512.
- Renier, L. A., Anurova, I., De Volder, A. G., Carlson, S., VanMeter, J., & Rauschecker, J. P. (2010). Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. *Neuron*, 68, 138–148.
- Röder, B., Stock, O., Bien, S., Neville, H., & Rösler, F. (2002). Speech processing activates visual cortex in congenitally blind humans. *European Journal of Neuroscience*, 16, 930–936.
- Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M.-P., Dold, G., et al. (1996). Activation of the primary visual cortex by braille reading in blind subjects. *Nature*, 380, 526–528.
- Saffran, J. R. (2003). Musical learning and language development. *Annals of the New York Academy of Sciences*, 999, 397–401.
- Schalk, G., Kapeller, C., Guger, C., Ogawa, H., Hiroshima, S., Lafer-Sousa, R., et al. (2017). Facephenes and rainbows: Causal evidence for functional and anatomical specificity of face and color processing in the human brain. *Proceedings of the National Academy of Sciences, U.S.A.*, 114, 12285–12290.
- Sharma, J., Angelucci, A., & Sur, M. (2000). Induction of visual orientation modules in auditory cortex. *Nature*, 404, 841–847.

- Sigalov, N., Maidenbaum, S., & Amedi, A. (2016). Reading in the dark: Neural correlates and cross-modal plasticity for learning to read entire words without visual experience. *Neuropsychologia*, 83, 149–160.
- Siuda-Krzywicka, K., Bola, Ł., Paplińska, M., Sumera, E., Jednoróg, K., Marchewka, A., et al. (2016). Massive cortical reorganization in sighted braille readers. *eLife*, 5, e10762.
- Striem-Amit, E., & Amedi, A. (2014). Visual cortex extrastriate body-selective area activation in congenitally blind people “seeing” by using sounds. *Current Biology*, 24, 687–692.
- Striem-Amit, E., Cohen, L., Dehaene, S., & Amedi, A. (2012). Reading with sounds: Sensory substitution selectively activates the visual word form area in the blind. *Neuron*, 76, 640–652.
- Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabrègue, R., Amadon, A., et al. (2011). Specialization for written words over objects in the visual cortex. *Neuroimage*, 56, 330–344.
- Szwed, M., Qiao, E., Jobert, A., Dehaene, S., & Cohen, L. (2014). Effects of literacy in early visual and occipitotemporal areas of Chinese and French readers. *Journal of Cognitive Neuroscience*, 26, 459–475.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B. H., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, 311, 670–674.
- Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, 31, 411–437.
- Vaden, K. I., Jr., Muftuler, L. T., & Hickok, G. (2010). Phonological repetition-suppression in bilateral superior temporal sulci. *Neuroimage*, 49, 1018–1023.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron*, 55, 143–156.
- Whitney, C. (2001). How the brain encodes the order of letters in a printed word: The SERIOL model and selective literature review. *Psychonomic Bulletin & Review*, 8, 221–243.
- Wimmer, H., Ludersdorfer, P., Richlan, F., & Kronbichler, M. (2016). Visual experience shapes orthographic representations in the visual word form area. *Psychological Science*, 27, 1240–1248.

Uncorrected Proof